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CONTRIBUTION TO A REVISION OF THE EARTHWORM
FAMILY OCNERODRILIDAE. THE GENUS *NEMATOGENIA*.

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No.4 — *Contribution to a revision of the earthworm family
Ocneroдрilidae.*

The genus NEMATOGENIA.

By G. E. GATES

INTRODUCTION

Since 1900, three supposedly endemic ocneroдрilids have been added to the long list (*cf.* Gates, 1942a) of North American species known only from types or original material. Three exotic species have been recorded (Gates, 1954, pp. 245-246) from the mainland or a neighboring island.

The casual spoil of other collecting (as so often in the past) now has made possible, for the first time in nearly six decades, some advance in our understanding of an important constituent of the oligochaete fauna of the continent.

The author's thanks are extended to Dr. P. J. Darlington, Jr., and to Dr. G. E. Pickford, for the opportunity of studying these interesting earthworms.

Genus NEMATOGENIA Eisen, 1900

Ocneroдрilus (Nematogenia) Eisen 1900, Proc. California Ac. Sci., (3) 2, p. 112. (Type species, *Pygmaeodrilus lacuum* Beddard, 1893.)

Nematogenia, Michaelsen, 1900, Das Tierreich, 10, p. 376.

Nematogenia, Stephenson, 1930, The Oligochaeta, p. 862.

The genus has been defined (Stephenson, 1930) essentially as follows: Dorsal pores present. Male pores, united with apertures of the single pair of prostates, on xvii. Spermathecae, adiverticulate, one pair, with pores on or behind 8/9. Gizzards, two, in vi-vii. Calciferous sacs, one pair, in ix. Metandric. Accordingly, two, three or four characters contraindicate inclusion of the Hispaniolan species, described below. Admission to all other ocneroдрilid genera is, by definition, also denied. Erection of at least two new genera is required by previous practice. Re-examination of the basis of classification of the family, however, first seems preferable.

Ocneroдрilid genera have been defined (*cf.* Stephenson, 1930, pp. 856-863) by the following characters; closeness of pairing

of setae, presence or absence of dorsal pores, presence or absence of ectal union of male deferent ducts with ducts of one pair of prostates, number of spermathecae and location of the spermathecal pores, number and location of gizzards, number and location of calciferous glands, presence or absence of diverticula on the spermathecal duct, number and location of prostates, andry (number and location of testes). However, little importance seems to have been attached to somatic structure. Calciferous glands and gizzards are not mentioned in the definition of *Pygmaeodrilus*, and species of *Gordiodrilus* may have a pair of lateral saes or a single, median and ventral one, as well as one, two or no gizzards. Several genera have the same gizzard or calciferous-gland characters. Dorsal pores are present, in the Afro-American portion of the family (that with extramural calciferous glands), only in two species. Setal pairing is not mentioned in definitions of five of the genera recognized in 1930. Wide setal pairing, in anterior and middle regions of the body, has been reported from one species (Seychelles), in middle and posterior regions of the body, from two species (South America). Obviously, then, division of the family into genera has been based mainly on the genital organs.

The reproductive system, in all earthworm families, always has provided most of the characters for distinguishing and defining species. It is now being found that this system is "most susceptible to evolutionary change when reproduction is parthenogenetic" (Gates, 1956a, p. 227) for parthenogenesis permits more rapid accumulation of mutations. Such "evolutionary plasticity of the reproductive system necessitates considerable caution in use of its structures for taxonomic purposes at genus or higher level" (Gates, 1956b, p. 30).

Uniquely diagnostic somatic characters, in the Oligochaeta as known today, are very rare. None has been found in the Oenocordilidae. All species herein considered do, however, share a pair of somatic characters which are unknown in that combination elsewhere in the family. A combination of three genital characters, also found in each of the species herein considered is, however, shared with other groups that now have subgeneric or generic status. Obviously, then, since other characters are unavailable, the genus must be defined, at least primarily, by

somatic structure, as below. For the present, non-diagnostic but universally descriptive genital characters are retained in the definition. Latero-oesophageal hearts in x-xi appear to be characteristic in the family and need no mention.

Definition. Bithecal, pores at or behind 8/9. Biprostatic, pores on xvii. Male pores in or close to xvii.

Gizzards, two, in vi-vii. Calciferous glands, lateral, one pair, in ix. Spermathecae adiverticulate.

Distribution. Dominican Republic (Hispaniola).

The genus is known to be represented elsewhere only by a peregrine species formerly thought to be African but now apparently of American origin. This peregrine species extends the generic range to include the following: Panama, Costa Rica, Camerons, Fernando Po, Belgian Congo, Ceylon.

Key to species of NEMATOGENIA

1. a. Body small, less than three mm thick, dorsal pores present2
- b. Body larger, more than three mm thick, dorsal pores lacking.3
2. a. Spermathecal pores on 8/9, male deferent and prostatic ducts of a side unite in parietes to open by a common pore.*lacuum*
- b. Spermathecal pores midway between 8/9 and eq/ix, male pores discrete and behind prostatic pores.*panamaensis*
3. a. Typhlosole present4
- b. Typhlosole lacking5
4. a. Holandric*alba*
- b. Metandric*montana*
5. a. Intestinal origin in xii*magna*
- b. Intestinal origin in xiv*dominicana*

External characteristics that might provide a more useful key for preliminary identification are liable to individual variation. Until more is known about such differences, reliance on characters less liable to intraspecific variation is preferable. Deficiencies in our knowledge of species erected in the previous century complicate key construction and obviate any attempt to show phylogenetic relationships.

NEMATOGENIA MAGNA sp. nov.

Loma Rucilla, Cordillera Central, Dominican Republic, under grass in open pine woods at 8-10,000 feet, June 1938, 0-0-1. Dr. P. J. Darlington Jr. (Loma Rucilla is said to be the highest mountain in the West Indies.)

External characteristics. Length, 190 + mm (+ 70 mm?). Diameter, 8 mm. Segments, ca. 400 + (+ 129?). Pigmentation, unrecognizable (alcoholic preservation). Prostomium, prolobous. Secondary furrows; one well marked and postequatorial on each of iii-vii, one less distinct and pre-equatorial on each of v-vi, one pre-equatorial and one postequatorial deep furrow on each of viii-xiii. The posteriormost secondary annulus on each of ix-xi has a tertiary furrow. Nephropores and dorsal pores unrecognizable, the latter probably lacking.

Setae deeply retracted on preclitellar and clitellar segments, often unrecognizable, apparently small and not closely paired. Shortly behind the clitellum, $AB=CD < BC < AA$, $DD > \frac{1}{2}C$, but farther on $AB < CD < BC < AA$. Still more posteriorly AB ca. = BC = or slightly < or slightly > CD , AA appears to be consistently > BC throughout though the difference may be small. In xvii, *a* setae probably present but *b* setae lacking.

Clitellum red (preservation artefact?), annular, on xiv-xxviii, the posteriormost portion of xiii with a slight red coloration.

Sphermathecal pores, one pair, at or slightly median to *B*, on 8/9. Female pores widely separated, equatorial, at approximate sites of apertures of *a* follicles, on xiv. Male and prostatic pores discrete, the former diagonally slit-like, the others smaller, circular and anterior, all at or just lateral to *B* and in a single, transverse, smooth, glistening area with distinct anterior and posterior boundaries about at levels of 16/17 and 17/18. Lateral margins of the area indistinct but in *BC* and nearer *C*. The pores of each side are in a slight depression within an area of special tumescence that is most obvious in *AB*.

No other genital markings.

Internal anatomy. Septum 6/7 slightly muscular, 7/8-10/11 thickly muscular, 11/12 strengthened but translucent.

Gizzards large, in vi and vii. Calciferous glands one pair, in ix, of solid type (no lumen), large, lateromesially flattened, thickly discoidal, slightly notched ventrally. Duet fairly thick,

soft, from pointed dorsal apex of each gland to lateral face of gut shortly in front of 9/10, with rather large aperture into gut lumen. Longitudinal lamellae on inner wall of gut in front of gland apertures gradually disappear anteriorly in ix. Intestinal origin in xii. Typhlosole lacking but at mD on roof of gut for some distance behind lvi there is a very low ridge, round to triangular in cross section. Supra-intestinal gland, in several segments around clv, an obvious yellowish thickening of gut roof where the tissues have a honey-comb texture.

Dorsal blood vessel single, disappearing from view within the pharyngeal glands in iii. Ventral trunk unrecognizable anterior to vii. Subneural lacking or unrecognizable, extra-oesophageals not distinguishable. Supra-oesophageal recognizable only in ix where a large branch on each side passes laterally on dorsal face of calciferous gland stalk and then down into the gland. Commissures of vi-ix obviously connect dorsal and ventral trunks. Commissures, or hearts, of x-xi probably latero-oesophageal but there is no blood in either of the apparent dorsal bifurcations of each vessel. A small transversely placed body resting on the dorsal blood vessel but attached to the anterior face of each septum, from 50/51 posteriorly, resembles the "lymph" glands present in similar locations of certain species of the megascolecine genus, *Pheretima* Kinberg 1866.

Metandric. A longitudinal membrane on each side of the body between 10/11 and 11/12 just lateral to the testes and male funnel looks much like the wall of a testis sac but a roof was not found (testicular coagulum extending well upwards). Seminal vesicles, one pair, in xii, large, lobed. Prostates *ca.* 20 mm long, would reach into xlv at least if straight. A duct is not clearly marked off but may be about 3 mm long. The male deferent duct comes into contact with lateral face of the prostatic duct in xvii but is continued on slightly, somewhat thickened, before turning mesially to pass into the parietes just behind the prostatic duct.

Spermathecae, without diverticula or seminal chambers, *ca.* 6 mm long, flattened against the parietes back to 9/10 and with a slightly wider portion vertically flattened against anterior face of 9/10 to which the spermatheca is bound by connective tissue. Duct and ampulla are not distinctly demarcated ex-

ternally. If an ectal portion with thick wall and very small lumen is to be regarded as the duct, it then is much shorter than the ampulla. A terminal ental portion of the spermatheca is distended by a white coagulum.

Remarks. A tail portion had been recently broken off, presumably during collection. The hind end that was in the same tube may well be of the same worm though the jagged edges of the breaks do not exactly fit together. The clitellum is cracked in several places as often happens when worms are preserved with that organ in maximal tumescence. Except for local macerations of intestinal wall the specimen otherwise is in good condition.

A supra-intestinal gland of any kind has been unknown hitherto in any ocerodrilid. Its anatomy in *N. magna* needs characterization from microtome rather than freehand sections but now appears to be similar to that of the "grid" at end of the typhlosole in the octochaetine *Barogaster* Gates 1939. Supra-intestinal glands have not as yet been looked for in many earthworm genera. Hitherto the glands usually have been associated with the posterior end of a median typhlosole. In *Nematogenia*, however, the glands are present only when there is no typhlosole.

N. magna is distinguishable from all ocerodrilids, except two species of *Kerriona* Michaelsen 1924 and one of *Paulistus* Michaelsen 1925, by its size as well as segment number, and from the species of *Kerriona* and *Paulistus* by the presence of two gizzards (instead of none). A size of 260 x 8 mm, in a family where all species hitherto known, except those just mentioned, are 15-60 x 1-3 mm certainly is significant. Recognition of additional differences from other species of *Nematogenia* awaits more adequate characterization of those previously erected.

A species, when understood to be an interbreeding population of organisms with more or less individual if not also geographic variation, obviously cannot be defined from a single individual. Nevertheless, some sort of a concise characterization is needed. In such a precis it is also convenient to list characters, presumably of taxonomic importance, about which information is desired.

Precis. Spermathecal pores minute, superficial, slightly median to *B*, at 8/9. Female pores at sites of missing *a* setae. Male pores at or just lateral to *B* and shortly behind prostatic pores, both pores of a side in an area of special tumescence within a median field reaching laterally into *BC*. Clitellum, annular, on xiv-xxviii. Setae, not closely paired. (Nephropores? No dorsal pores.) Prostomium prolobous. (Pigmentation?) Segments, *ca.* 529. Size, 260 x 8 mm.

Intestinal origin in xii. (No typhlosole.) Supra-intestinal gland in region around 155th segment. Lymph glands present posteriorly. Metandric. Spermathecal duct shorter than ampulla.

NEMATOGENIA DOMINICANA sp. nov.

San Cristobal, Santo Domingo. From earth of damp forested hillside, July 19, 1930, 1-0-0. Damp soil in hills to west, July 20, 1930, 0-1-0. R. Bond per Dr. G. E. Pickford.

External characteristics. Length, *ca.* 195 mm. Diameter, 5+ mm. Segments, *ca.* 675 (No. 2). Pigmentation lacking ("grayish pink or pink, paler posteriorly," collector's note). Prostomium, broadly prolobous (No. 1) or indenting i (No. 2) and then slightly proepilobous. Secondary furrows; one deep and postsetal on each of vii-xiii, one deep and presetal on each of viii-xiii, less obvious pre- and postsetal secondary furrows recognizable back to xl. Each pre- and postsetal secondary annulus of ix-xi has a well marked tertiary furrow. Nephropores unrecognizable. Dorsal pores lacking.

Setae first certainly recognizable on ii or iii, very closely paired, *AB ca.*=*CD*, *BC* much < *AA*, *DD* > $\frac{1}{2}$ *C*, in xxv, *BC*:*AA*:5:7 gradually changing to 1:2 posteriorly, and thence on constant.

Spermathecal pores, one pair, at *B*, on 8/9. Female pores unrecognizable but possibly equatorial and in *AB* (*a* present) on xiv. Male and prostatic pores discrete, the former minute, circular, the others transversely slit-like and anterior, all about at *B* on xvii. Porophores transversely elliptical, flat but markedly protuberant, with center about at *B*, reaching into *AA* and to 17/18 but not to 16/17. A distinctly demarcated, smooth, small,

circular portion bearing the prostatic pore appears to be slightly retractile and the immediate margin of the pore is raised in a teat-like protuberance. The male pore is near the posterior margin of the porophore.

No other genital markings.

Internal anatomy. Septum 5/6 membranous, 6/7 slightly muscular, 7/8-11/12 thickly muscular and funnel-shaped.

Gizzards well developed, in vi-vii. Calciferous glands one pair, in ix, of solid type (no lumen), rather heart-shaped, with slight ventral indentation (not disc-shaped). Intestinal origin in xiv (2). Typhlosole lacking and no slightest rudiment recognizable from xiv-xl but from xli to lxvi there is a low, band-like area the wrinkled surface of which contrasts strikingly with the smoothness of other portions of the gut wall. The band gradually disappears but at mD a fine ridging still is recognizable and gradually passes into the supra-intestinal gland, a wide thickening of gut roof also ridged on ventral side. The gland extends from 180/181 to 194/195 (No. 1, *ca.* 365 segments) or from 187/188 to 208/209 (No. 2). The gland is slightly constricted at septal insertions (the juvenile) and has an appearance of being marked off into segmental glands.

Dorsal blood vessel single, disappearing from view in tissue masses of the pharyngeal bulb that reach to 5/6, in intestinal region receiving in each segment two pairs of large vessels from the gut, one pair near each septum. Supra-oesophageal trunk recognizable only in ix-xi, apparently ending with hearts of xi. Extra-oesophageals filled with blood and recognizable only in viii-ix where they are median to the hearts and free from the gut. A large vessel passes out from the supra-oesophageal in ix, on each side, and shortly bifurcates, one branch passing along calciferous duct to and into the gland, the other branch passing down to join the extra-oesophageal. Subneural quite unrecognizable (probably lacking?). Segmental commissures connecting dorsal and ventral trunks quite slender in v-vii, somewhat larger in viii-ix (lateral hearts?). Hearts of x-xi apparently latero-oesophageal but blood present only in the bifurcations that pass to the supra-oesophageal. Lymph glands present and apparently as in *magna*.

Metandric. Seminal vesicles, one pair, in xii. Prostates 18-20 mm long, would reach at least into xlv if straight, pink (formalin developed artefact?). An ectal white portion, slightly slenderer, 1-2 mm long, with marked muscular sheen constitutes the duct. The male deferent duct is thicker behind 16/17, in contact with lateral face of prostatic duct but continued on as in other species and is narrowed again within the parietes.

Spermathecae, 4+ mm long, without diverticula or seminal chambers, but with distinctly demarcated duct and ampulla. The latter, *ca.* 1 mm long, elliptical in cross section, *ca.* twice as thick as ental portion of duct, filled with a white coagulum. Duct, circular in cross section, very shortly and closely looped ectally.

Reproduction. Brilliant iridescence on male funnels and in spermathecal ducts ectally (but not in coagulum of spermathecal ampullae) shows that sperm had been matured and that copulation had been completed, in the larger specimen. Reproduction presumably is sexual and biparental.

Regeneration. Segment length, at 395/396, abruptly becomes very much shorter and so continues posteriorly, as in a tail regenerate.

Remarks. The acitellate worm had been ruptured in the intestinal region. No signs of postsexual regression were recognized in that worm which may have been preserved prior to development of the clitellum. In that case copulation takes place, as has been suggested for other species, before the clitellum develops.

Absence of a typhlosole and presence of a supra-intestinal gland indicate relationship to *magna* from which *dominicana* is distinguished as follows: By constant close pairing of setae throughout the body as well as other setal characters. Presence of paired male porophores. Intestinal origin in xiv (rather than xii), an important distinction in a family where the origin so very frequently is in xii. Greater length of spermathecal duct relative to that of the ampulla. Further differences may be recognizable when clitellate specimens become available.

Precis. Spermathecal pores minute, superficial, at *B*, on 8/9. Female pores in *AB*? Male pores about at *B*, shortly behind prostatic pores, in paired, transversely elliptical porophores.

(Clitellum?) Setae very closely paired, $BC < AA$, $DD > \frac{1}{2}C$. (Nephropores? No dorsal pores.) Prostomium probolous. Unpigmented (?). Segments, 675. Size, 195 x 5 mm.

Intestinal origin in xiv. (No typhlosole.) Supra-intestinal gland in ten or more segments behind 180/181. Lymph glands present posteriorly. Metandric. Spermathecal duct longer than ampulla, ectally with short loops.

NEMATOGENIA MONTANA sp. nov.

Loma Rucilla, Cordillera Central, Dominican Republic, under grass in open pine woods at 8-10,000 feet, June 1938, 0-0-2. Dr. P. J. Darlington Jr.

External characteristics. Length, 85 and 108 mm. Diameter, 4 mm (clitellum). Segments, 178 and 144 (± 1 , a metameric anomaly). Pigmentation, unrecognizable (alcoholic preservation). Prostomium, probolous (2 specimens). Secondary furrows, one presetal and one postsetal each on vii-ix. Nephropores and dorsal pores unrecognizable, the latter probably lacking.

Setae closely paired anterior to clitellum, more widely paired behind clitellum, farther posteriorly AB ea.=or $< CD < BC < AA$, DD =or slightly $< \frac{1}{2}C$.

Clitellum white, annular, from 13/14 onto anterior portion of xxi (No. 1) or to 21/22 (No. 2), intersegmental furrows present (No. 1) or lacking (No. 2), setae probably present.

Spermathecal pores, one pair, about at B , on anterior margin of ix. Female pores, probably slightly anteromedian to a setae, on xiv. Male and prostatic pores unrecognizable but presumably in or near a small indistinctly demarcated white area in AB , on xvii.

No other genital markings.

Internal anatomy. Septa 5/6-11/12 muscular to thickly muscular.

Gizzards well developed, in vi and vii. Calciferous glands, one pair, in ix, of solid type (no lumen), sausage-shaped, opening through a short stalk from dorsal end into oesophagus anterior to 9/10. Intestinal origin in xiii (2). Typhlosole begins rather gradually in region of xvii-xxii, reaching maximum height (0.75 mm) in xxv-xxvi, lamelliform, apparently ending abruptly in lxxxvii (No. 1) or ciii (No. 2) though more careful examination

reveals a rudimentary continuation that gradually diminishes and is unrecognizable behind xcv (No. 1) or cxv (No. 2). Supra-intestinal gland lacking.

Vascular system, with latero-oesophageal hearts in x-xi, no subneural, but with "lymph" glands, and, so far as can be determined, as in *magna*.

Metandrie. Seminal vesicles, one pair, lobed, in xii. Prostates *ca.* 14 mm long, would reach at least into region of xxxviii-xl if straight (duct indistinguishable externally), passing into parietes at *B*. Male deferent duct just lateral to prostate in xvii, and only well behind ectal portion of that gland turning mesially to pass, slightly widened, into parietes about at *A* and just in front of level of 17/18.

Spermathecae, without diverticula or seminal chambers. Ampullae, on anterior face of 9/10, clearly demarcated from a slender duct that may be nearly as long as the ampulla or somewhat shorter.

Reproduction. Iridescence on male funnels, in spermathecal ducts and in coagulum of each spermathecal ampulla is brilliant and demonstrates maturation of sperm as well as completion of copulation. Reproduction presumably is sexual and biparental.

Regeneration. The penultimate segment of each worm is large and setigerous. The anal "segment" is unusually small, scarcely more than a narrow band around a vertically slit-like anal aperture. Such an anal band, without pigment, develops in pigmented species shortly after posterior amputation and is quite different at that stage from the normal anal region.

Segment cii of No. 1 is only about half as long as ci and succeeding segments for some distance are of the same length. The region behind 101/102 would have been suspected of being a regenerate except for the increase in length of the last few segments.

Parasites. Cysts are scattered through the coelomic cavities of a posterior portion of the body in one worm.

Remarks. *N. montana* is clearly distinguished from *magna* by the much smaller size, shorter clitellum, presence of a typhlosole, and absence of a supra-intestinal gland. Distinctions from *dominicana* are: much smaller number of segments, wider pairing of setae behind the clitellum, shorter and unlooped spermathecal

duct, intestinal origin in xiii instead of xiv, presence of a typhlosole, and absence of a supra-intestinal gland. The only differences from the inadequately characterized *panamaensis* that can be cited at present are: greater size (rather than 35-75 x 1-2 mm), larger number of segments (rather than 110-120), absence of dorsal pores, wider pairing of setae behind the clitellum. Presumably closest relationships are with *panamaensis*.

Absence of male funnels, or any rudiments thereof, in segment x of this and the two preceding species appears to be indicative of long establishment of the metandry.

Procis. Spermathecal pores minute, superficial, about at *B*, on anterior margin of ix. Female pores anteromedian to *a* (?). Male pores behind prostatic pores which are also in *AB* (no porophores or male field?). Clitellum, annular, on xiv-xxii. Setae more widely paired behind clitellum, $AB = \text{or} < CD < BC < AA$, $DD = \text{or} < \frac{1}{2}C$. (Nephropores? No dorsal pores.) Prostomium probolous. (Pigmentation?) Segments, 144-178. Size, 85-105 x 4 mm.

Intestinal origin in xiii. Typhlosole simply lamelliform. (No supra-intestinal gland.) Lymph glands present posteriorly. Metandric. Spermathecal duct, about as long as ampulla, slender.

NEMATOGENIA ALBA sp. nov.

Loma Rucilla, Cordillera Central, Dominican Republic, under grass in open pine woods at 8-10,000 feet, June 1938, 1-3-2. Dr. P. J. Darlington Jr.

External characteristics. Length, 95-115 mm. Diameter, 4-4+ mm. Segments, 211, 213, 230. Pigmentation, unrecognizable (alcoholic preservation). Prostomium, tanylobous, a definite transverse furrow across the tongue shortly behind anterior margin of i (2 specimens) produces a condition that can be designated as combined tany- and epiloby. Secondary furrows, one presetal and one postsetal on some or all of viii-xi. Nephropores and dorsal pores unrecognizable, the latter probably lacking.

Setae begin on ii and are closely paired, on xx $AB \text{ ca.} = CD < BC$ much $<$ or $= AA$, $DD \text{ ca.} =$ or slightly $< \frac{1}{2}C$.

Clitellum red, annular, on xiii-xx (1), setae present, intersegmental furrows obliterated except that a slight trace of 13/14 is still recognizable in ventrum.

Spermathecal pores, one pair, very small, transverse slits, on or just lateral to *B*, definitely though only slightly behind 8/9. Female pores, minute, diagonal slits, in front of *a* setae. Male and prostatic pores discrete, in seminal furrows. One limb of each furrow is about on *A* between level of 17/18 (unrecognizable in ventrum) and eq/xvii, the other limb passing almost at a right angle laterally along eq/xvii to *B*. The male pore is at the posterior end of the groove. The prostatic pore has not been seen but the prostatic duct has been traced through the body wall to anterior end of the groove. Each seminal furrow is in a small region of special tumescence reaching from about *mBC* median to *A*, to eq/xviii but not to level of 16/17. Both tumescences, on the clitellate worm, are within a single transverse field.

No other genital markings.

Internal anatomy. Septum 6/7 membranous or only very slightly strengthened, (5/6?), 7/8-11/12 slightly muscular and translucent.

Gizzards well developed, apparently in vi-vii. Calciferous glands, one pair, in ix, of solid type (no lumen), ovoidal, with rather short but thick stalk from dorsal apex passing to lateral face of oesophagus anterior to 9/10. Oesophagus valvular through xiii (3). Intestinal origin in xiv (3), the real origin concealed by symmetrical or asymmetrical herniation of intestine through 13/14 well into xiii. Typhlosole rudimentary in xv-xix, gradually becoming lamelliform and attaining maximum height (1 + mm) in xix-xx, gradually losing height posteriorly and unrecognizable behind 158/159 (juvenile with 230 segments), 140/141 (211 segments, posterior amputee?), or 143/144 (213 segments, apparently with a very small anal-segment regenerate) and in this worm ending abruptly rather than gradually and indefinitely. Supra-intestinal gland lacking.

Vascular system with latero-oesophageal hearts in x-xi, no sub-neural (lymph glands?); otherwise, so far as can be determined, as in *magna*. Nephridia present from ii, ducts (behind the clitellum) pass into parietes in *AB*.

Holandric. Seminal vesicles in ix and xii. Those of ix may be much larger, extending anteriorly into vii but in a worm with right posterior vesicle continued into xv, the left anterior

vesicle is confined to ix. Prostates, 17+ mm long, would reach into lx if straight, elliptical in cross section and with slit-shaped lumen. An ectal portion *ca.* two mm long, with muscular sheen, circular in cross section, with narrower lumen, is the duct. Male deferent duct lateral to the prostate in xvii, posteriorly turning mesially to pass into parietes at level of 17/18 about at A. slightly thickened just prior to entrance into parietes.

Spermathecal duct about as long as ampulla from which it is clearly demarcated by a definite constriction, thicker entally and there elliptical in cross section, with a slit-shaped lumen, ectal portion circular in cross section and with much smaller lumen. Coagulum that fills the ampulla is without iridescence. The iridescence that characterizes the ental portion of the duct is recognizable in transverse sections only in a jagged circle apparently at the middle of the wall.

Reproduction. Brilliant iridescence on male funnels and in ental portions of spermathecal ducts (acelitellate and clitellate worms) shows that sperm had been matured and that copulation had taken place. Reproduction presumably is sexual and biparental.

Remarks. The clitellum of one worm listed as clitellate actually is only slightly developed.

Prostates of one worm pass straight forward into viii instead of posteriorly as usual.

The cuticle was found, several years after the Hispaniolan worms were dissected, to be loosened from the epidermis in various small portions of the body. Removal of loosened patches permitted, in better conditions, another search for nephropores. None was found in three species. Possible sites in *N. alba* may be as follows: At or slightly above *D* and near anterior segmental margins, on iii-ix or x. Posteriorly, on segmental equators (but with some irregularity?) and just median to *D*.

Male maturity, here as in *dominicana*, apparently may be reached and copulation completed before appearance of the clitellum. The latter organ, at full development, is indicative primarily of female maturity. Copulation may even be a prerequisite for clitellar development.

N. alba is distinguished from all species hitherto referred to the genus by its holandry, from all American species by the

presence of seminal grooves, and, with exception of *montana*, by the presence of a typhlosole. Further distinctions from *montana* are provided by the intestinal origin in xiv, and the prostomium.

Precis. Spermathecal pores small transverse slits, at or just lateral to *B*, slightly behind 8/9. Female pores in front of *a*. Male pores in posterior ends of seminal grooves, about at *A* and 17/18. Male field transverse, seminal grooves along *A* from 17/18 to eq/xvii and thence to *B*. Clitellum, annular, on xiii-xx. Setae, closely paired, $AB=CD$, $BC < \text{or} = AA$, $DD \text{ ea} = \frac{1}{2}C$. (Nephropores? No dorsal pores.) Prostomium tanylobous but with tongue crossed by a transverse furrow. (Pigmentation?) Segments, 211-230. Size, 95-115 x 4 mm.

Intestinal origin in xiv. Typhlosole vertically lamelliform. (No supra-intestinal gland. Lymph glands?) Holandric. Seminal vesicles in ix and xii. Spermathecal duct about as long as ampulla, thicker entally.

NEMATOGENIA LACUUM Beddard, 1893

Pygmacodrillus lacuum Beddard 1893, Quart. J. Micr. Sci., 34, p. 259, figs. 13-16 (pl. 26). (Type locality, supposedly Lagos in West Africa. Types, if extant, in the British Mus.)

Oenerodrillus lacuum, Beddard, 1895, Monog. Oligochaeta, p. 515.

Nematogenia lacuum, Michaelsen, 1900, Das Tierreich, 10, p. 376.

This taxon, unfortunately, was made the type species. It is known only from the original description of "five or six" specimens supposedly from Lagos (West Africa) but collected alive at Kew in England. The anatomy was determined from sections partly ruined by sand which presumably had not been cleared out from the gut. No information is available as to nephropores, female pores, male field, typhlosole, supra-intestinal glands, major blood vessels, hearts.

The species always has been assumed to be endemic in Africa.

Precis. Spermathecal pores in *AB*, at 8/9. (Female pores?) Male pores, apertures of united male deferent and prostatic ducts, in *AB*, in oval elevations in xvii. Clitellum, saddle-shaped, on xiii/2-xxvi/2. Setae closely paired, *ab*/xvii-xviii lacking. (Nephropores?) Dorsal pores present, beginning at 6/7 or even anteriorly. Prostomium prolobous(?). (Pigmentation?) Segments, ca. 120. Size, 25 (x 1+?) mm.

Intestinal origin in xii. (Typhlosole? Supra-intestinal gland? Lymph glands? Hearts?) Metandric. Seminal vesicles in xii. Small bulbus ejaculatorius present.

Spermathecal duct slender, longer than the ampulla.

Distribution. Unknown. (See above.)

NEMATOGENIA PANAMAENSIS Eisen, 1900

- Oenocrodrilus (Nematogenia) lacuum* var. *panamaensis*, Eisen 1900, Proc. California Ac. Sci., (3) 2, p. 127, figs. 55-65 (pl. 9), 114-116 (pl. 11). (Type locality, Panama. Types, if extant, probably in U. S. Nat. Mus.)
- Nematogenia panamaensis*, Michaelsen, 1900, Das Tierreich, 10, p. 376.
- Nematogenia panamaensis*, Michaelsen, 1903, Ark. Zool. 1, p. 163. (Camer-oons)
- Nematogenia panamacensis*, Michaelsen, 1904, Sitzber. Böhm. Ges. Prag, 1903, (40), p. 16. (Ceylon)
- Nematogenia josephina* Cognetti, 1904, Boll. Mus. Torino, 19, (478), p. 3. (Type locality, San Jose, Costa Rica. Types in Torino Mus.?)
- Nematogenia josephina*, Cognetti, 1906, Mem. Ac. Sci. Torino, 56, p. 55.
- Nematogenia (sic) panamaensis*, Cognetti, 1908, Ann. Mus. Genova, (3), 4, p. 33. (Fernando Po)
- Nematogenia panamaensis*, Michaelsen, 1915, Ergeb. 2 Deutschen Zentral-Afrika-Exp. 1910-11, 1, (Zool. 1), p. 222. (Belgian Congo)
- Nematogenia panamaensis*, Stephenson, 1923, Oligochaeta, in Fauna British India, p. 483.

Prostomium, female pores, typhlosole, lymph and supra-intestinal glands, hearts and other portions of the vascular system, in the original description, were not mentioned. Nor have most of those deficiencies as yet been rectified. A blood vessel in segment xii is indeed labelled heart (Eisen, 1900, fig. 56h, pl. 9) but none was shown in xi where a pair certainly is present. Hearts in xii, in the Oenocrodrilidae, would be so unusual that abnormality or a mistake in drawing must, in absence of subsequent confirmation, be assumed.

Male pores are discrete. Hence, a statement to the contrary (and applicable only to *lacuum*) in the generic definition always has been unwarranted.

Sperm were seen by Eisen in the spermathecal ampulla. Reproduction, since sperm are matured and exchanged in copulation, can be assumed to be sexual and biparental.

N. josephina is distinguished from *panamaensis*, according to its author (Cognetti, 1906, p. 57) by location of the first dorsal

pore (at 8/9 instead of 10/11), length of prostates, and absence of hearts in xii. The first two characters, in better known species, are subject to considerable individual variation and the third difference probably is not real. If spermathecal pores were correctly located by Cognetti, at 8/9, there would be reason for believing some distinct status eventually might be justified.

N. panamaensis is peregrine, in the sense usually intended by that word in oligochaetological literature, the overseas discontinuities in its distribution due to transportation, presumably by man and since the days of Henry the Navigator. The discrete male pores (if valid evidence of relationship) then require, instead of an African origin as previously maintained, one in America.

Precis. Spermathecal pores in *AB*, midway between 8/9 and eq/ix. (Female pores anterior to *a*?) Male pores behind prostatic pores, in a single pair of porophores. Clitellum (shape?), in xiii, xiii/n, xiv-xxi, xxii/n. Setae, closely paired, *a,b*/xvii lacking. Nephropores at *D*. Dorsal pores beginning at or behind 8/9. (Prostomium? Pigmentation?) Segments 110-120. Size, 37-55 x 1-2 mm.

Intestinal origin in xiii. (Typhlosole? Supra-intestinal and lymph glands?) Metandric. Spermathecal duct slender, shorter than ampulla.

Distribution. Panama, Costa Rica (San Jose), Cameroons (Bange, Bibundi, Buea, Victoria, Musake), Fernando Po, Belgian Congo (Kongo da Lemba and St. Joseph on the Luala River), Ceylon (Peradeniya).

Key to genera of the Oenerodrilidae*

1. *a.* Extramural calciferous glands lacking ... 2
- b.* Extramural calciferous glands present 3
2. *a.* One gizzard, in vii *Malabaria, Thatonia.*
- b.* Two gizzards, in vi-vii *Deccania.*
3. *a.* Calciferous sacs paired, lateral 4
- b.* Calciferous sacs unpaired, median and ventral 8

* *Malabaria, Thatonia, Deccania* are known only from India and Burma *Mahcina* only from the Seychelles (to which it may have been transported recently), *Curgiona* only from India (to which it may have been introduced recently). *Gordiodrillus* (as of Michaelsen & Stephenson) is African. Other genera are American or American and African.

4. a. Calciferous saes in ix and x5
 b. Calciferous saes in ix only6
5. a. One gizzard, in vi *Maheina*.
 b. No gizzard *Paulistus, Quechuona*.
6. a. One or more gizzards7
 b. No gizzards *Ocnodrilus*, including
Liodrilus, Haplodrilus,
Ilyogenia, as well as
Pygmaeodrilus, Eukerria (part), *Dia-*
phorodrilus, Kerriona.
7. a. One gizzard, in vii *Eukerria* (as it must be
 restricted).
 b. Two gizzards, in vi-vii *Nematogenia*.
8. a. Calciferous saes in ix-x, (gizzard in vii) ... *Curgiona*.
 b. Calciferous saes in ix9
9. a. One or more gizzards10
 b. No gizzard *Gordiodrilus* (part),
 as it must be
 restricted.
10. a. One gizzard, in viii *Gordiodrilus*, a
 "robustus" group of
 species.
 b. Two gizzards, in vii-viii *Gordiodrilus*, a
 "nannodrilus" group
 of species.

DISCUSSION

A taxonomy based primarily on genital structure culminated, in the Ocnodrilidae, in the congeries known as *Gordiodrilus* (cf. Gates, 1942b, pp. 75-85). That taxonomic waste-basket which defeated Stephenson, "I can do nothing with this heterogeneous group" (1930, p. 863), probably could have been avoided (Gates, 1942b, p. 76) if somatic structure had been taken into consideration, even as little as previously. Collections that would justify a real attempt at revision of *Gordiodrilus*, unfortunately, are no more available now than in 1942.

Errors of typography, observation and interpretation, so frequent in the literature on *Gordiodrilus*, may well be much less common in the literature on other ocnodrilid genera. Nevertheless, more adequate characterization of somatic systems still is

prerequisite to a revision of any portion of the family. Also needed is information as to individual and geographical variation about which next to nothing is now known.

Some of the taxonomic changes that will be made in the future can be deduced from a key constructed entirely on characters supplied by just one somatic system. That is the digestive system. The organs involved are gizzards and calciferous glands, with the glands having the greater importance.

Genera that key out together are presently distinguishable from each other only by means of characters furnished by the system usually most liable to rapid evolutionary change. The genital characters by which those genera are defined and distinguished, elsewhere in the family and/or in other families, do not, and sometimes cannot, have that taxonomic value.

Relationships suggested by somatic systems are of course often different from those that were deduced in the past from reproductive structure. Thus *Diaphorodrilus* now seems to be closer to *Ocnerodrilus* than to *Gordiodrilus* with which it was mistakenly united. *Kerriona* may be closer to *Ocnerodrilus* than to its supposed ancestor *Kerria*.

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